The number of species and subspecies in the Red-bellied Pitta *Erythropitta erythrogaster* complex: a quantitative analysis of morphological characters

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We examined specimens representing 29 of the 31 taxa described in the Red-bellied Pitta *Erythropitta erythrogaster* complex, in the wake of a primarily molecular study that concluded 17 species are involved. Using quantitative criteria we evaluated the morphological (plumage and mensural) characters of each taxon to determine its taxonomic rank. We found that 13 taxa (*erythrogaster, inspeculata, caeruleitorques, palliceps, celebensis, dohertyi, rufiventris, rubrinucha, macklotii, meeki, gazellae, splendida* and *novaehibernicae*) scored sufficiently highly to be considered species. Nine (*cyanonota, bernsteini, piroensis, digglesi, habenichti, loriae, oblita, finschii* and *extima*) emerged as subspecies, and nine others (*yairocho, propinqua, obiensis, kuehni, aruensis, strenua* and *yorki*, plus the unseen but uncontroversial *thompsoni* and *inornata*) are treated as synonyms. Thus morphology conforms with 75% of splits generated by mainly molecular insights. Further changes to the proposed arrangement may, of course, occur with new evidence, notably acoustic.

INTRODUCTION

For several decades taxonomists and ornithologists have treated the Red-bellied Pitta *Pitta* (now *Erythropitta*: see Irestedt *et al.* 2006) *erythrogaster* as a single species comprising as many as 26 subspecies scattered across the islands between the Philippines and Solomons (Mayr 1979, Lambert 1996, Erritzoe & Erritzoe 1998, Erritzoe 2003). In morphology the taxa comprising this radiation are united by several characters—blue breast-band, blue wings and tail, and red belly—but marked out by differences in size and in the colours of the upperparts, throat, ear-coverts, crown, nape and lower breast, in a broad suite of combinations. Indeed, the degree of phenotypic variation exhibited by most of these subspecies has been acknowledged as unusually high (Lambert 1996, Erritzoe 2003), and one of the taxa, *dohertyi* from the Sula Islands east of Sulawesi, is so distinctive that it has sometimes been separated out as a full species (Sibley & Monroe 1990, Lambert 1996, Inskipp *et al.* 1996, BirdLife International 2001), although to do so in isolation seems both biogeographically problematic and taxonomically invidious. In the absence of tools or rules by which to attempt a comprehensive revision of the species, the taxonomic default position has understandably been to leave the entire complex alone.

With the advent of molecular analysis, however, a tool emerged for the assessment of degree of relatedness between taxa. Taking an 'integrative' approach—led by genetic evidence but complemented by morphological and partial vocal information—Irestedt *et al.* (2013) produced a revolutionary arrangement in which the Red-bellied Pitta breaks down into 17 species. However, despite the commendable thoroughness and clarity of this study, its conclusions have not been adopted by Dickinson & Christidis (2014) or Gill & Donsker (2015). Moreover, several very able ornithologists with experience of many taxa in the complex indicated to us in personal communications that the vocal similarities between the newly defined species are sufficiently strong to represent a real source of unease about the proposed new arrangement, if vocal differentiation is considered a decisive measure of speciation under the Biological Species Concept (BSC).

Adoption of a phylogenetic species concept (PSC) approach to the issue would result, we assume, in every diagnosable taxon—hence every recognised subspecies—in the complex being elevated to species rank, and with up to 26 subspecies generally considered valid this would be closer to the conclusions reached by Irestedt *et al.* (2013); but such a move would only be appropriate (albeit still not necessarily right) if all other diagnosable taxa in the class Aves were subject to the same criteria. Without specifying a particular species concept in support of their revision, Irestedt *et al.* (2013) evidently declined a PSC approach, implying instead that the use of as many lines of evidence as possible had produced an arrangement which approximated to biological species limits: 'If differences in plumage and vocalizations provide cues for species recognition, then most of the species that we recognize are likely to be reproductively isolated'.

The perennial difficulty of determining reproductive isolation in closely related allopatric taxa renders it impossible to decide with confidence on biological species status, and Irestedt *et al.* (2013) were impressively undogmatic and open in the way they offered their revision to the world. The only drawback to their analysis, if it *is* a drawback, resides in the use of 'most' in the quotation above: it implies variable performance in meeting a particular standard by the taxa they elevate to species rank. We therefore sought to review the *Erythropitta erythrogaster* complex from an independent perspective using another new tool, the criteria for species delimitation set out by Tobias *et al.* (2010).

METHODS

Although the criteria in Tobias *et al.* (2010) provide for the analysis of acoustic, behavioural and ecological evidence, the necessary material for a full set of comparisons is unavailable. We therefore considered the issue of species rank among the Red-bellied Pitta complex using only morphological (plumage and morphometric) evidence. We examined museum specimens in the American Museum of Natural History (AMNH), New York, USA, Natural History Museum, Tring, UK (NHMUK, but BMNH for catalogue numbers), Naturalis, Leiden, Netherlands (RMNH for catalogue numbers) and Zoologisches Museum, Berlin, Germany (ZMB). We took photographs of representative samples of taxa and used them when making comparisons in the other museums. For morphometric analysis we used the very thorough tables (with their means and standard deviations) provided by Erritzoe & Erritzoe (1998), who measured much the same material; in a few cases we supplemented these data with measurements of our own (these cases are identified; unattributed measurement-related data refer to the Erritzoes' work). We also referred to the diagnoses provided by the SOM in Irestedt *et al.* (2013).

As far as we are aware, the total number of taxa that have been ascribed to the Red-bellied Pitta is 31, all mentioned and 26 regarded as valid by Mayr (1979; for ranges see Figure 1). In the following list, we give after each taxon (a) the number of adult specimens of both sexes examined at our principal research base, NHMUK,

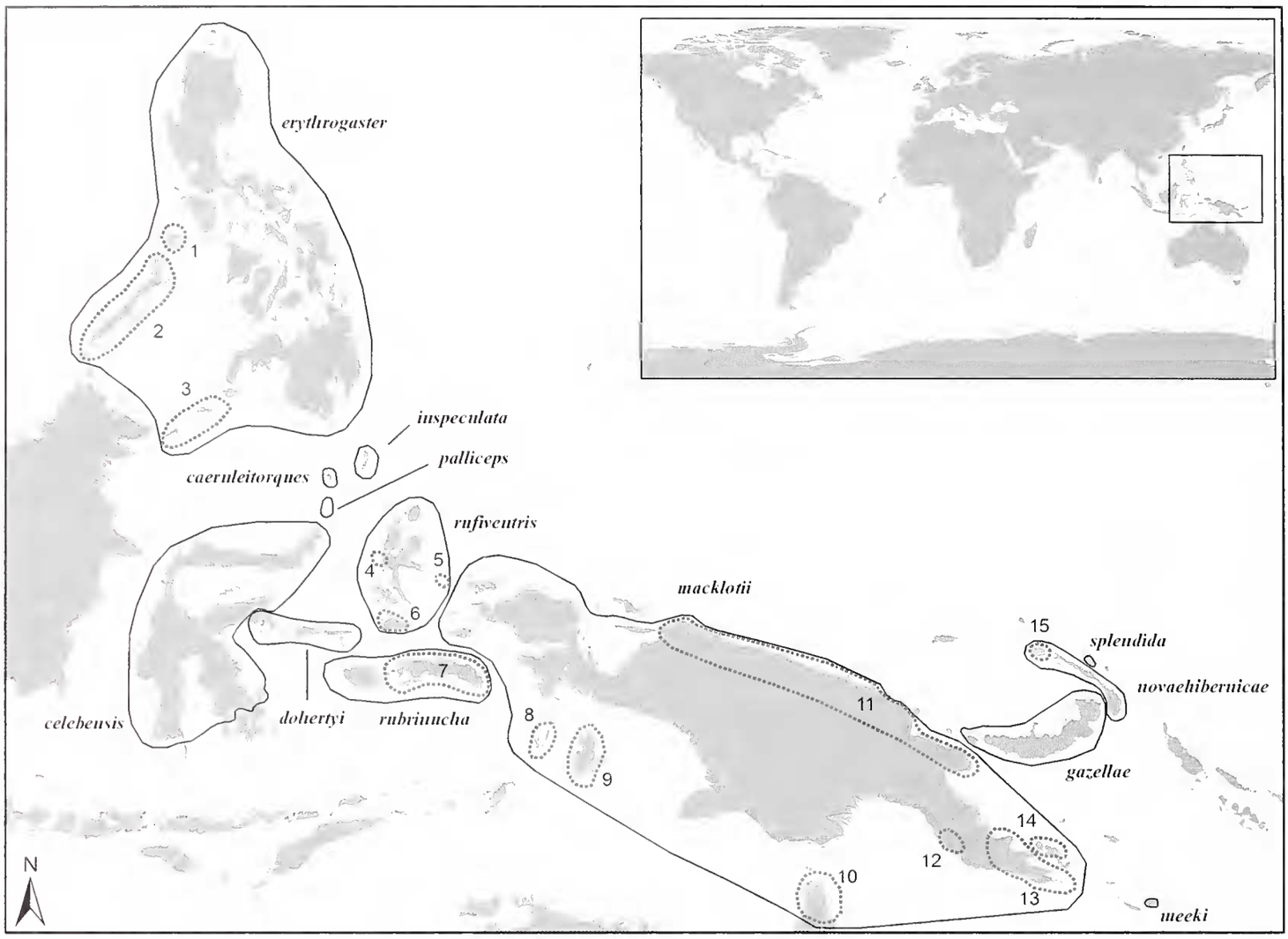


Figure 1. The distribution of taxa in the Red-bellied Pitta complex, based on analyses in this paper. Solid lines define ranges of species, with name of species adjacent. Dotted lines define ranges of other taxa, numbered as follows (inverted commas indicating taxa not considered valid here): 1, *'thompsoni'*; 2, *'propinqua'*; 3, *'yairocho'*; 4, *cyanonota*; 5, *bernsteini*; 6, *'obiensis'*; 7, *piroensis*; 8, *'kuehni'*; 9, *'aruensis'*; 10, *digglesi*; 11, *habenichti*; 12, *oblita*; 13, *loriae*; 14, *finschii*; 15, *extima*. Three other invalid taxa (*'inornata'*, *'strenua'*, *'yorki'*) are not represented as they reflect no geographical information.

with an asterisk (*) indicating that the total includes the type, (b) in brackets the number of specimens (sexes here conflated) for which morphometric data were provided by Erritzoe & Erritzoe (1998), with ranges when some variables could not be measured, and (c) the number of specimens of certain taxa that were examined in the other three museums (we did not keep a full tally of specimens considered in these institutions as we were mainly targeting those taxa for which NHMUK holds little or no material): *erythrogaster* 30 (52–58), *thompsoni* 0 (1), *propinqua* 7 (13–15), *yairocho* 0 (0) 4, *inspeculata* 3 (14–20) 8, *caeruleitorques* 0 (2) 2, *palliceps* 0 (4) 8, *celebensis* 12 (31–43), *dohertyi* 1 (3–6) 4, *rufiventris* 11 (24–31), *obiensis* 1 (3–5) 3, *inornata* 1* (0), *cyanonota* 4* (7), *bernsteini* 0 (2) 1, *rubrinucha* 2* (4) 2, *piroensis* 0 (3) 4, *macklotii* 67 (50–56), *kuehni* 3 (30–35) >20, *aruensis* 5 (2), *strenua* 1* (0), *digglesi* 0 (0), *yorki* 0 (0), *habenichti* 1 (24–29) >40, *loriae* 12 (29–31), *oblita* 0 (5) 4, *finschii* 6 (15) >10, *extima* 1 (8–9) 12, *meeki* 3 (19) 13, *gazellae* 8 (79–85), *splendida* 0 (13) 12 and *novaehibernicae* 0 (10–11) >15. Thus we examined all described taxa except *thompsoni* and *yorki*.

We measured the degree of phenotypic distinctiveness of each taxon using a system in which an exceptional difference (a radically different coloration, pattern or vocalisation) scores 4, a major character (pronounced difference in body part colour or pattern, measurement or vocalisation) 3, a medium character (clear difference reflected, e.g., by a distinct *hue* rather than different colour) 2, and a minor character (weak difference, e.g. a change in shade) 1; a threshold of 7 is set to allow species status, species status cannot be triggered by minor characters alone, and only three plumage characters, two vocal characters, two biometric characters (assessed for effect size using Cohen's *d* where 0.2–2 is minor, 2–5 medium, 5–10 major and >10 exceptional) and one behavioural or ecological character may be counted (Tobias *et al.* 2010). Where additional characters are apparent but under these rules cannot be scored, the formula 'ns[1]' is used, signalling 'not scored' but giving in parenthesis the estimated value of the difference in question. Where the sample size of measurements was too small to generate a standard deviation, we use personal judgement in order to 'allow' a score; unless otherwise stated, mensural comparisons are between males.

We compared taxa with each other until they failed to reach a score of 7. Some taxa failed at the first comparison, while others, even if their relatedness appeared unlikely on biogeographical grounds, continued to be compared until all options were exhausted.

Taxa in the Red-bellied Pitta complex generally have a small white spot midway along the central primaries, and variations in position, size and existence of this spot have been used taxonomically (the name *inspeculata* indicates the absence of the spot in Talaud birds). However, we found the documentation of this variable difficult and unrewarding, and elected to set it aside as a line of inquiry.

RESULTS

Of the 29 taxa in the Red-bellied Pitta complex which we reviewed directly, 13 scored sufficiently highly against the Tobias criteria to be considered species, nine emerged as subspecies, and seven were

found or confirmed to be synonyms. Of the two taxa not examined, the case for their synonymisation prevailed.

In the following accounts the scores for each of the accepted species are provided in round brackets at the end of each character description, with the total score in square brackets at the end of the entry. All subspecies composing polytypic species were taken account of in the comparisons we made.

Erythropitta erythrogaster Philippine Pitta

This form differs from other taxa in the complex by its combination of green breast-sides, buff-streaked throat, blue upper mantle above green dorsum, and dark lateral crown-stripes with no blue in the central crown (see under other species for Tobias scores).

Erythropitta inspeculata Talaud Pitta

Differs from *E. erythrogaster* (morphologically the closest taxon) by its all cobalt-blue (no green) upperparts and breast-sides (3), plain dark brown crown *vs* paler brown crown with dark brown lateral stripes (3), much reduced or no white in centre of black throat (1), stronger red belly (ns[1]), bill on average longer (in RMNH four males 23.5 *vs* six males from Mindanao 22.3: NJC) and wings distinctly shorter (same birds 92 *vs* 98.6) (for latter allow 1) [8];

and from *E. caeruleitorques*, *E. palliceps*, *E. celebensis*, *E. dohertyi*, *E. rufiventris*, *E. rubrinucha*, *E. macklotii*, *E. meeki*, *E. gazellae*, *E. splendida* and *E. novaehibernicae* by characters itemised under those species.

Erythropitta caeruleitorques Sangihe Pitta

Differs from *E. erythrogaster* by its lack of blackish lateral stripes (2), paler, much brighter rest of crown (3), blue-green *vs* half-green, half-blue upperparts (below blue upper mantle) (ns[1]), variably broad/narrow black lower breast-band (ns[1]), unstreaked, paler throat (2), deeper bill (allow 1) [8];

from *E. inspeculata* by its plain pale reddish-brown crown *vs* chocolate-brown crown (3), pale brown *vs* black ear-coverts to chin and upper throat (3), green-blue *vs* blue upperparts (2), slightly longer tarsus (allow 1) [9];

from *E. celebensis* by its lack of electric-blue coronal stripe (3), plain pale reddish-brown crown *vs* dark brown crown-sides shading to ferruginous nape (3), blue-green *vs* green upperparts (1), shorter wing (allow 1), longer bill (allow 1) [9];

from *E. rufiventris* by its black *vs* grey-brown lower throat and upper breast (3), blue band across upper mantle (2), paler, more uniform crown with much less grey-brown on frontal half (2) [7];

from *E. meeki* by its blue-green *vs* green upperparts (2), darker, narrower blue breast (2), generally narrower black lower breast-band (ns[1]), bright fulvous-rufous *vs* dull ochreish-brown crown (ns[1]), stronger black upper breast-patch (1) and considerably shorter bill and tail (allow 2) [7];

and from *E. palliceps*, *E. dohertyi*, *E. rubrinucha*, *E. macklotii*, *E. gazellae*, *E. splendida* and *E. novaehibernicae* by characters under those species.

Erythropitta palliceps Siao Pitta

Differs from *E. erythrogaster* by its electric-blue coronal stripe (3), lack (or only trace) of blue upper mantle (2), narrow black lower breast-band (2), lack of green breast-sides (ns[2]), unstreaked throat (ns[2]), considerably larger size (allow 2) [9];

from *E. inspeculata* by its much more developed electric-blue coronal stripe (ns[2]), pale rufous-brown *vs* dark chestnut rest of crown (3), dull green *vs* dull blue upperparts (3), pale brown *vs* black chin and throat (3) [9];

from *E. caeruleitorques* by its electric-blue coronal stripe *vs* none (3), much darker brown on forecrown and mid-crown (2), smaller black upper breast-spot (ns[1]), paler blue breast (1), greener upperparts (ns[1]) and longer wing (allow 1) [7];

from *E. celebensis* by paler lateral crown with cheek and throat less grey, more cinnamon-fulvous, so that head colour is rather uniform, with greater extension of brown from nape onto mantle, making a broader brown hindcollar *vs* darkish brown and chestnut on crown with contrasting much paler, buffier cheek and throat, with black hindcollar (3), much less developed electric-blue coronal stripe (2), smaller black patch on lower throat/upper breast and narrower (or no) black lower breast-band (2); slightly paler, more olive-green upperparts (ns[1]) [7];

from *E. meeki* by its electric-blue coronal stripe *vs* none (3), much narrower black lower breast-band (2), mid-brown *vs* grey-brown face and throat (1), longer wing (allow 1) and shorter bill (allow 1) [8];

and from *E. dohertyi*, *E. rufiventris*, *E. rubrinucha*, *E. macklotii*, *E. gazellae*, *E. splendida* and *E. novaehibernicae* by characters under those species.

Erythropitta celebensis Sulawesi Pitta

Differs from *E. erythrogaster* by its broad electric-blue coronal stripe (3), lack of blue upper mantle but narrow black hindcollar (ns[2]), richer chestnut hindcrown (ns[1]), (longitudinally) broader, brighter blue breast (2), broad black band below breast (2), less streaked throat (ns[1]) and rather larger size (effect size for wing 3.14, score 2) [9];

from *E. inspeculata* by its green *vs* blue upperparts (3), much broader, brighter blue breast (ns[2]), broad electric-blue coronal stripe *vs* none (3), bold black lower breast-band *vs* none (ns[2]), much paler head-sides and throat (ns[2]), paler chestnut crown-sides and nape with dark lateral crown-stripes *vs* none (3) [9];

from *E. rufiventris* by its strong electric-blue coronal stripe *vs* none (3), dark lateral crown-stripes *vs* none (2), blackish lower throat and upper breast with extension in weak line around hindneck *vs* small dark grey-brown lower throat-patch with no hindneck line but brighter rufous lower nape (3), dull blue *vs* dull green wing-coverts (ns[2]) [8];

from *E. rubrinucha* by its lack of a bold reddish-pink nuchal spot (3), chestnut *vs* dark brown hindcrown and nape (2), lack of (or vestigial) extended electric-blue ear-coverts (2) and longer wing (effect size 2.73; score 2) [9];

and from *E. caeruleitorques*, *E. palliceps*, *E. dohertyi*, *E. macklotii*, *E. meeki*, *E. gazellae*, *E. splendida* and *E. novaehibernicae* by characters under those species.

Erythropitta dohertyi Sula Pitta

Differs from all other taxa in complex (male plumage characters unless otherwise stated) by its broad black hind-collar (3), pale iris in female (3), paler blue breast, with notably broad lower black band (2), and slightly scaled pattern on upperparts (ns[1]) [8].

Erythropitta rufiventris North Moluccas Pitta

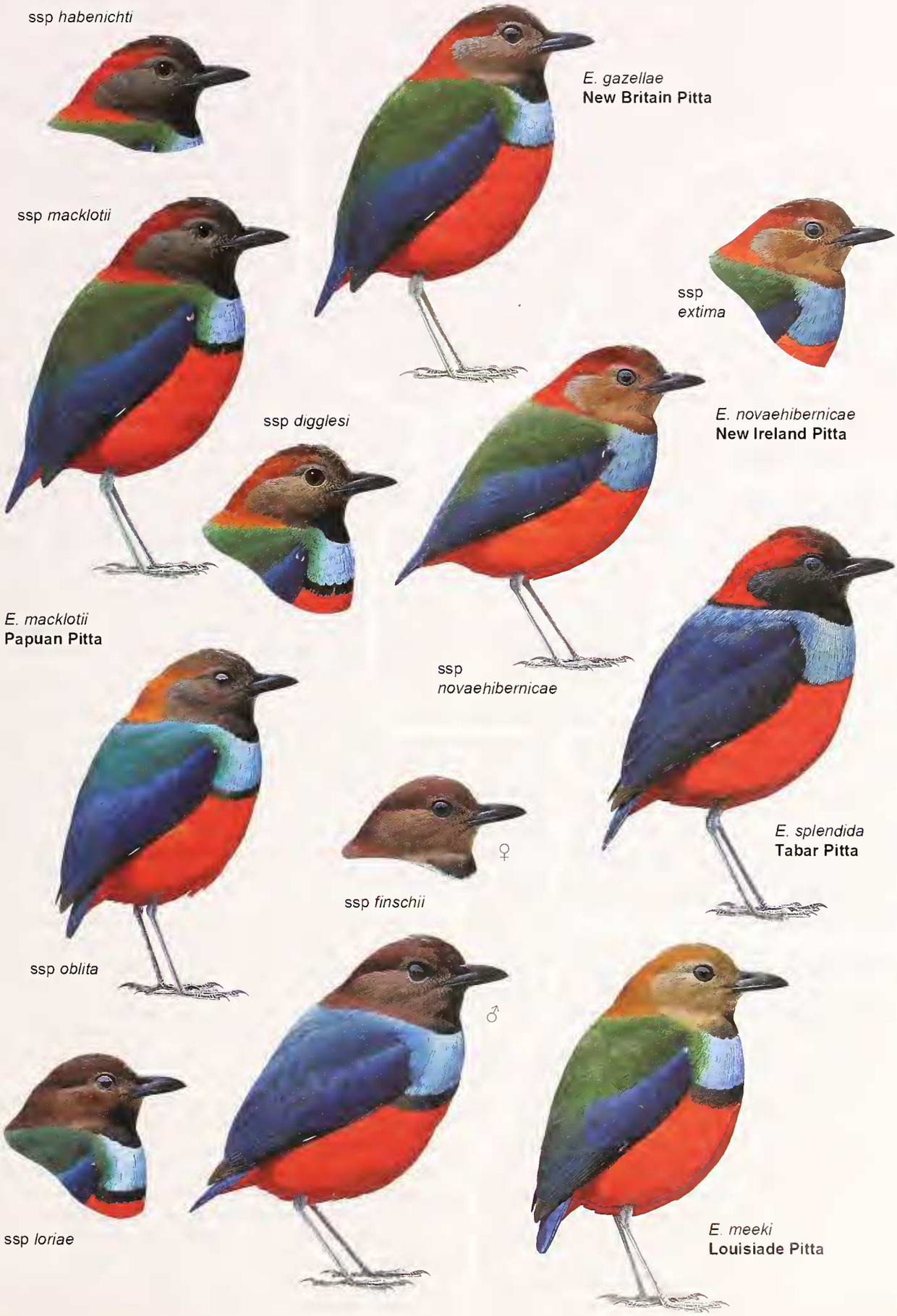
Including the forms *cyanonota* and *bernsteini*, differs from *E. erythrogaster* by its at most diffuse dusky-brown *vs* black upper breast-patch (2), no or greatly reduced green on breast-sides (2), no blue upper mantle (ns[2]), much darker green upperparts extending to rump (blue in *erythrogaster*) (3), brighter crown (ns[1]), shorter wing (effect size −1.2, score 1) but longer bill and tarsus (effect size for male tarsus 3, score 2) [10];

from *E. inspeculata* by its green *vs* blue upperparts (3), much broader, paler breast (2), pale brown *vs* (dark brown to usually) black throat and upper breast (3), paler, redder crown and nape (ns[2]) [8];

from *E. palliceps* by its lack of a broad electric-blue coronal stripe (3), mid-brown *vs* black patch on lower throat and upper breast (2), reduced narrow blackish breast-band (1), shorter wing (allow 2) [8];

from *E. rubrinucha* by its lack of an electric-blue coronal stripe (3), plain reddish-brown *vs* chocolate-brown crown (ns[2]), lack of bold reddish-pink nuchal patch (3), lack of elongate electric-blue ear-coverts (3) [9];

Plate 1. Taxa in the Red-bellied Pitta complex by Chris Rose, with adjustments by FJ.


ssp *habenichti*
E. gazellae
New Britain Pitta
ssp *macklotii*
ssp
extima
ssp *digglesi*
E. novaehibernicae
New Ireland Pitta
E. macklotii
Papuan Pitta
ssp
novaehibernicae
E. splendida
Tabar Pitta
♀
ssp *finschii*
ssp *oblita*
♂
ssp *loriae*
E. meeki
Louisiade Pitta

and from *E. caeruleitorques*, *E. celebensis*, *E. dohertyi*, *E. macklotii*, *E. meeki*, *E. gazellae*, *E. splendida* and *E. novaehibernicae* by characters given under those species.

Erythropitta rubrinucha South Moluccas Pitta

Including the form *piroensis*, differs from all taxa by its bold reddish-pink nuchal spot (3) and

from *E. erythrogaster* by its broad electric-blue coronal stripe (3), darker brown crown (ns[2]), extended electric-blue ear-coverts (3), darker green upperparts (ns[1]), no (or very reduced) green breast-sides (ns[2]), unstreaked throat (ns[2]), longer bill, tarsus and tail (effect size for tarsus 2.54, score 2) [11];

from *E. inspeculata* by its green *vs* blue upperparts (3), broad electric-blue coronal stripe (3), extended electric-blue ear-coverts (ns[3]), broader, paler blue breast (ns[2]), pale grey-buff *vs* blackish throat (ns[3]), darker brown crown (ns[1]) [9];

from *E. caeruleitorques* by its broad electric-blue coronal stripe (3), extended electric-blue ear-coverts (3), dark brown *vs* pale reddish-brown crown (ns[3]), lack of broad blue band across upper mantle (ns[2]), green *vs* blue-green remaining upperparts (ns[2]) [9];

from *E. palliceps* by its extended electric-blue ear-coverts (3), dark *vs* pale brown crown and nape (2), considerably shorter wing (allow 2) [10];

from *E. macklotii* by its broad electric-blue coronal stripe *vs* diffuse, weak and dull blue coronal area (ns[2]), extended electric-blue ear-coverts *vs* none (3), pale grey-brown *vs* blackish throat (3), narrow or non-existent blackish-green *vs* bold black breast-band (ns[2]), smaller size (effect size for wing −2.6, score 2) [11];

and from *E. celebensis*, *E. dohertyi*, *E. rufiventris*, *E. gazellei*, *E. splendida* and *E. novaehibernicae* by characters given under those species.

Erythropitta macklotii Papuan Pitta

Including the forms *digglesi*, *habenichti*, *loriae*, *oblita*, *finschii* and *extima*, differs from *E. erythrogaster* by its black throat and malar region (3), no green sides to blue breast (2), broad black lower breast-band *vs* none (3), black forecrown shading to dark brown or strong flame-red on nape (ns[2]), lack of blue upper mantle (ns[2]), darker green back with reduced area of blue on rump (ns[2]), considerably larger size (effect size for tarsus 3.7, score 2) [10];

from *E. inspeculata* by its (comparison here with morphologically closest form *finschii*) broader, paler blue breast (2), much broader black lower breast-band (2), paler, more chestnut hindcrown (1) and much larger size (effect size for wing 5.1, score 3) [8];

from *E. caeruleitorques* by its dark brown crown (with or without flame-red nape) *vs* uniform pale red-brown crown (2), blackish *vs* pale brown throat to ear-coverts (3), broader black lower breast-band (2), considerably larger size (allow 2) [9];

from *E. palliceps* by diffuse bluish coronal area *vs* clear broad electric-blue coronal stripe (2), darker brown crown (with or without flame-red nape) (2), blackish *vs* pale brown throat to ear-coverts (3), slightly larger size (ns) [7];

from *E. celebensis* by lack of broad electric-blue coronal stripe (3), blackish *vs* pale grey-brown throat to ear-coverts (3), blacker frontal half of crown (1), longer bill (effect size using nominate 2.7, score 2) [9];

from *E. rufiventris* (comparing morphologically closest nominate) by its blacker frontal half of crown (2), strong blue wing-coverts (2), blackish *vs* paler brown throat and ear-coverts (ns[2]), black *vs* paler dusky-brown upper breast-patch (3), much bolder and blacker lower breast-band (ns[2]), much longer wing (effect size using nominate 4.4, score 2) [9];

from *E. meeki* by very dark brown forecrown and richer red-chestnut hindcrown (with or without flame-red nape) *vs* uniform pale ochreish-brown crown (3), blackish *vs* pale greyish-brown throat to ear-coverts with darker black upper breast-patch (3), narrower (albeit broad) black lower breast-band (1), longer wing (effect size using nominate 2.29, score 2) [9];

from *E. gazellae* by very diffuse (sometimes vestigial or even absent) bluish coronal area *vs* broad electric-blue coronal stripe (2), lack (or vestigial presence) of elongate bluish ear-coverts (2), hindcrown and nape weaker red (ns[1]), broader, blacker lower breast-band (2), deeper bill (effect size using nominate 2.83, score 2) [8];

from *E. splendida* by lack of silvery-blue elongate ear-coverts (3), no narrow black hindcollar (2) and (in all taxa except *E. m. finschii*) green *vs* blue upperparts (3) or (in *E. m. finschii*) lack of bright flame-red mid-crown to nape (3) [8];

from *E. novaehibernicae* by lack of elongate pale blue ear-coverts (3), bold black lower breast-band (2), black *vs* pale brown throat, malar and upper breast-patch (3), blackish *vs* maroon frontal half of crown (ns[1]), much longer wing (effect size using nominate 3.4, score 2) [10];

and from *E. dohertyi* by characters listed under that species.

Erythropitta meeki Louisiade Pitta

Differs from *E. erythrogaster* by its lack of blackish-brown lateral crown-stripes (2), pale brown (extension from nape) *vs* blue upper mantle (2), darker upperparts (ns[1]), no green on breast-sides (ns[2]), very broad black lower breast-band *vs* none (3), larger size (effect size for tail 4.3, score 2) [9];

from *E. inspeculata* by its much paler, more ochreish-brown crown extending more onto nape (3), green *vs* blue upperparts (3), pale grey-brown *vs* blackish lower face, chin and upper throat-patch (ns[3]), broader, paler blue breast (ns[3]), bold black breast-band *vs* none (3), larger overall size with notably longer tail (effect size 3.84, score 2) [11];

from *E. celebensis* by its lack of broad electric-blue coronal stripe (3), paler, more ochreish crown, the colour extending onto nape where *celebensis* has a blackish hindcollar (3), smaller, weaker upper breast-patch (2), broader black lower breast-band (ns[1]), shorter wing (effect size −2.5, score 2) but longer bill (effect size 3.5, score 2) [12];

from *E. rufiventris* by its more ochreish crown with no strong reddish-rufous nape (2), small blackish breast-patch *vs* none (3), very broad black lower breast-band *vs* vague greenish-black line (3), larger size (effect size for wing 2.46, score 2) [10];

from *E. rubrinucha* by its lack of electric-blue coronal stripe (3), pale *vs* dark brown crown to nape (ns[3]), lack of reddish-pink nuchal spot (3), weaker elongate pale blue ear-coverts (ns[2]), broad black lower breast-band *vs* none (3), larger size (effect size for bill 2.5, score 2) [11];

from *E. gazellae* by its lack of electric-blue coronal stripe (3), lack of bluish elongate ear-coverts (ns[2]), pale ochreish- *vs* dark brown frontal half of crown (2), pale ochreish-brown *vs* bright chestnut to flame-red distal half of crown to nape (3), pale brownish throat with small blackish breast-patch *vs* black throat and broad black upper breast-patch (ns[2]), much broader lower breast-band (ns[2]), somewhat shorter wing (effect size −2.4, score 2) but slightly longer bill (effect size 1.24, score 1) [11];

from *E. splendida* by its ochreish-brown *vs* frontally maroon, distally bright red crown (3), green *vs* blue upperparts (3), weak (brownish) *vs* strong black throat and breast-patch (3), broad *vs* very narrow black lower breast-band (ns[3]), and considerably shorter wing (effect size −4.7, score 2) [11];

from *E. novaehibernicae* by its ochreish-brown *vs* frontally maroon, distally flame-red crown (3), green *vs* blue rump (ns[2]), less developed pale blue ear-coverts (ns[1]), grey-brown *vs* warm pale brown face and chin (ns[1]), blackish *vs* mid-brown upper breast-patch (3), broad black lower breast-band *vs* none (3) [9];

and from *E. caeruleitorques*, *E. palliceps*, *E. dohertyi* and *E. macklotii* by characters given under those species.

Erythropitta gazellae New Britain Pitta

Differs from *E. erythrogaster* by its electric-blue coronal stripe *vs* none (3), blackish frontal and bright chestnut to flame-red distal crown *vs* chestnut-brown crown with darker lateral stripes (3), lack of blue upper mantle (ns[2]), darker green upperparts with less blue around rump (ns[2]), bluish elongate ear-coverts *vs* none (3), blackish throat and breast-patch *vs* pale-streaked brown throat and smaller breast-patch (ns[2]), narrow *vs* broad green breast-sides (ns[2]), blackish lower breast-band *vs* none (ns[2]), larger overall size (effect size for tarsus 4.2, score 2) [11];

from *E. caeruleitorques* by its electric-blue coronal stripe *vs* none (3), blackish *vs* pale ochreish- or rufous-brown frontal half of crown (3), flame-red *vs* pale ochreish- or rufous-brown distal half of crown (3), lack of vague blue upper mantle (ns[2]), green *vs* green-blue upperparts (ns[2]), bluish elongate ear-coverts *vs* none (ns[3]), greyer face (ns[1]), blackish *vs* pale brown throat (ns[2]), longer tail and tarsus (allow at least 1) [10];

from *E. inspeculata* by its much stronger electric-blue coronal stripe (ns[2]), bright chestnut to flame-red *vs* dark chestnut hindcrown and nape (3), green *vs* blue upperparts (3), pale brownish *vs* black face and chin (3), moderately broad blackish lower breast-band *vs* none (ns[2]), longer wing (effect size 3.8, score 2) [11];

from *E. palliceps* by its flame-red *vs* ochreish-brown hindcrown (3), bluish elongate ear-coverts *vs* none (2), black throat and broad black upper breast-patch *vs* pale brown throat with small black breast-patch (3) [8];

from *E. celebensis* by its less developed electric-blue coronal stripe (2), bright chestnut to flame-red *vs* rufous-chestnut (with black collar) hindneck and nape (ns[2]), bluish elongate ear-coverts *vs* none (3), grey-brown *vs* pale buff face and chin (2), weaker blackish lower breast-band (ns[1]), larger bill (effect size for depth 2.3, score 2) [9];

from *E. rufiventris* by its electric-blue coronal stripe *vs* none (3), blackish frontal and bright chestnut to flame-red distal crown to nape *vs* overall reddish-rufous crown (ns[2]), bluish elongate ear-coverts *vs* none (3), black throat and breast-patch *vs* none (3), broader blackish lower breast-band (ns[1]), considerably longer wing (effect size 4.8, score 2) [11];

from *E. rubrinucha* by its flame-red *vs* dark brown (with reddish-pink nuchal spot) hindcrown and nape (3), black throat and broad breast-patch *vs* pale grey-brown throat and small black breast-patch (3), broader blackish lower breast-band (1), considerably longer wing (effect size 2.6, score 2) [9];

from *E. splendida* by its electric-blue coronal stripe *vs* none (3), flame-red *vs* bright red hindcrown and nape (1), green *vs* blue upperparts (3), paler face and chin (ns[1]) and smaller overall size (effect size for tarsus –2.3, score 2) [9];

from *E. novaehibernicae* by its relatively strong electric-blue coronal stripe (2), darker and narrower (black of crown extending further back) bright chestnut to flame-red hindneck (1), black *vs* pale brown throat and mid-brown breast-patch (3), considerably longer wing (effect size 3.6, score 2) [8];

and from *E. dohertyi*, *E. macklotii* and *E. meeki* by characters given under those species.

Erythropitta splendida Tabar Pitta

Differs from *E. erythrogaster* by its blackish forecrown and bright red hindcrown *vs* chestnut-brown crown with darker lateral stripes (3), lack of bright blue upper mantle (ns[2]), blue *vs* green upperparts (3), black chin to breast-patch *vs* pale brown chin and throat and small black breast-patch (3), no green breast-sides (ns[2]), narrow black lower breast-band *vs* none (ns[1]), much larger size (effect size for tarsus 6.45, score 3) [12];

from *E. inspeculata* by its blackish *vs* deep chestnut forecrown (1), bright red *vs* deep chestnut hindcrown and nape (3), broader, paler blue breast (2), narrow black lower breast-band *vs* none (ns[1]), much larger size (effect size for wing 6.75, score 3) [9];

from *E. caeruleitorques* by its blackish *vs* pale ochre forecrown (ns[2]), bright red *vs* pale ochre hindcrown and nape (3), elongate electric-blue ear-coverts *vs* none (3), black *vs* pale brown face and chin (3), larger size (allow 2) [11];

from *E. palliceps* by its weak and dull *vs* strong electric-blue coronal stripe (ns[2]), bright red *vs* ochreish hindcrown and nape (3), blue *vs* green upperparts (3), black *vs* mid-brown lower face, chin and throat (3), somewhat larger bill (allow 1) [10];

from *E. celebensis* by its blue *vs* green upperparts (3), weak, dull and diffuse *vs* strong electric-blue coronal stripe (ns[2]), maroon *vs* dull brown forecrown (ns[1]), bright red *vs* pale chestnut hindcrown and nape (3), elongate electric-blue ear-coverts *vs* none (3), strong black chin to upper breast-patch *vs* pale grey-brown chin and small blackish breast-patch (ns[3]), no green breast-sides (ns[2]), notably larger bill and longer tarsus (effect size for tarsus 4.16, score 2) [11];

from *E. rufiventris* by its blue *vs* green upperparts (3), maroon *vs* dull reddish-brown forecrown (ns[1]), bright red *vs* pale reddish-chestnut hindcrown and nape (3), elongate electric-blue ear-coverts *vs* none (3), strong black chin to upper breast-patch *vs* pale grey-brown chin to breast-patch (ns[3]), much longer wing (effect size 6.07, score 3) [12];

from *E. rubrinucha* by its blue *vs* green upperparts (3), weak and dull *vs* strong electric-blue coronal stripe (ns[2]), bright red hindcrown to nape *vs* dark brown hindcrown with reddish-pink nuchal spot (3); strong black chin to upper breast-patch *vs* pale grey-brown chin to weak blackish breast-patch (3), larger overall size (effect size for wing 3, score 2) [11];

from *E. meeki* by its blue *vs* green upperparts (3), maroon *vs* pale ochreish-brown forecrown (ns[2]), bright red *vs* pale ochreish-chestnut hindcrown and nape (3), strong black chin to upper breast-patch *vs* pale grey-brown chin to weak blackish breast-patch (3), very narrow *vs* very broad black lower breast-band (ns[3]), overall larger size (effect size for wing 3.13, score 2) [11];

from *E. novaehibernicae* by its blue *vs* green upperparts (3), darker maroon forecrown and brighter red hindcrown (2), blackish *vs* pale grey-brown face and throat and mid-brown breast-patch (3), narrow *vs* no black lower breast-band (ns[1]) and much longer wing (effect size 5.36, score 3) [11];

and from *E. dohertyi*, *E. macklotii* and *E. gazellae* by characters given under those species.

Erythropitta novaehibernicae New Ireland Pitta

Differs from *E. erythrogaster* by its maroon frontal and flame-red distal crown to nape *vs* chestnut-brown crown with darker lateral stripes (3), lack of blue upper mantle (ns[2]), elongate pale blue ear-coverts *vs* none (3), unstreaked pale brown throat and no black upper breast-patch (3), no broad green breast-sides (ns[2]), longer tarsus (effect size 3.6, score 2) [11];

from *E. inspeculata* by its maroon *vs* dark chestnut frontal half of crown (ns[1]), flame-red *vs* dark chestnut distal half of crown to nape (3), green *vs* blue upperparts (3), elongate pale blue ear-coverts *vs* none (3), pale grey-brown *vs* blackish face to upper breast-patch (ns[3]), broader, paler blue breast (ns[2]), overall somewhat larger size (effect size for tail 2.58, score 2) [11];

from *E. caeruleitorques* by its maroon *vs* ochreish- or rufous-brown frontal half of crown (ns[2]), flame-red *vs* ochreish-brown distal half of crown to nape (3), green *vs* greenish-blue upperparts (ns[2]), elongate pale blue ear-coverts *vs* none (3), lack of black upper breast-patch (3) [9];

from *E. palliceps* by its vestigial or absent electric-blue coronal stripe (ns[2]), flame-red *vs* ochreish-brown distal half of crown to nape (3), elongate pale blue ear-coverts *vs* none (3), lack of black upper breast-patch (3), lack of narrow black breast-band (ns[2]), shorter wing (at least 2) [11];

from *E. celebensis* by its vestigial or absent *vs* strong electric-blue coronal stripe (3), flame-red *vs* chestnut distal half of crown to nape

(3), elongate pale blue ear-coverts *vs* none (3), lack of black upper breast-patch (ns[3]), less green on breast-sides (ns[1]), no *vs* broad black lower breast-band (ns[3]), shorter wing (effect size −3.66, score 2) but longer bill and tarsus (effect size for bill 2.06, score 2) [13];

from *E. rufiventris* by its elongate pale blue ear-coverts *vs* none (3), flame-red *vs* reddish-chestnut hindcrown and nape (2), blue *vs* green rump (2), slightly longer wing (effect size 0.52, score 1) [8];

from *E. rubrinucha* by its vestigial or absent electric-blue coronal stripe (2), flame-red *vs* dark brown distal half of crown to nape (3), blue *vs* green rump (ns[2]), lack of blackish upper breast-patch (3) and slightly longer tail and tarsus (effect size for tarsus 1.3, score 1) [9];

and from *E. dohertyi*, *E. macklotii*, *E. meeki*, *E. gazellae* and *E. splendida* by characters under those species.

Taxa judged species by Irestedt *et al.* (2013)

Four taxa treated as species by Irestedt *et al.* (2010) were assigned to subspecies under the Tobias criteria, owing to their reduced degrees of morphological distinctiveness.

Taxon *yairocho*.—This is a curious case, in that the only two sources to recognise the form, Hachisuka (1935), who described it (from the Sulu Islands in the Philippines), and Irestedt *et al.* (2013), who split it, used plumage diagnoses that do not overlap. Hachisuka (1935) treated it as a subspecies of *erythrogaster*, the male differing 'in having an entirely black patch on throat, with no trace of white; chin and crown also dark smoky brown', the female differing merely in that 'the throat is more smoky chestnut and the white is restricted to the base of the feathers, so that normally this is not seen'. However, Irestedt *et al.* (2013), while rescuing *yairocho* from synonymy with *E. e. erythrogaster* where it was placed by Mayr (1979) and Dickinson *et al.* (1991), diagnosed it as having 'longer scapulars, tertials and rump green, thus green equally extensive as in other taxa with green upperparts; breast entirely green, without blue on central breast'. The Irestedt account appears to be based on two specimens in Naturalis (RMNH 121390, male, and 121391, female; both from Jolo, a range extension), which do indeed have the breast entirely green; but this happens in *erythrogaster* also (e.g. RMNH 121389), while the type of *yairocho*, in AMNH, and a specimen from Sibutu (ZMB 32342) have a dull blue central breast with green sides, as in most *erythrogaster*. The measurement of the scapulars is difficult and would need validation in a larger sample, besides which they represent an improbable specific character; and the green rump and tertials are not diagnostic. Meanwhile, Hachisuka's all-black throat-patch in the male sometimes also occurs in *erythrogaster* (e.g. BMNH 80.11.18.52, 91.5.13.518), while RMNH 121391 and ZMB 32342 have a distinctly visible whitish central throat-patch and the former's throat is exactly the same brown colour as, e.g., RMNH 92861 from Luzon. Measurements (by NJC) of the two Naturalis and single ZMB birds coincide closely with those of birds from Mindanao. Thus, discounting length of scapulars, there appears to be no dependable morphological character on which to base *yairocho*.

Taxon *piroensis*.—Seemingly high variation in the very small sample of both this taxon (from Seram) and *rubrinucha* (three and four specimens measured respectively in Erritzoe & Erritzoe 1998) plagues diagnoses and makes it hard to determine real distinctions between these taxa. The 'absence of the black line separating the silvery blue-gray of the breast from the scarlet belly' is noted in the original description (Muir & Kershaw 1910), but this line is 'a few mm wide or virtually absent' in Irestedt *et al.* (2013) while it is actually rather broad and bold in the only two adult specimens in AMNH. The latter authors mention 'a few feathers on central crown sometimes with faint indication of sky-blue margins', but the two AMNH specimens have more than a 'few' crown feathers with far more than 'faint' indications of blue, although the colour is diffused across the central and rear crowns and is certainly not a stripe. The chief difference lies in the laterally broad but vertically narrow reddish-pink nape *vs rubrinucha*'s reddish-pink nuchal spot surrounded by brown (score 3). Other characters may be (a) the more extensive pale blue ear-coverts, adjoining the area behind the eye and even extending narrowly above it (present in three of four adult specimens examined, in AMNH and Naturalis); and (b) the presence and distribution of white in the wing (*fide* Muir & Kershaw 1910, Irestedt *et al.* 2013). However, until a review can be made of all available specimens of the two taxa, preferably backed by information from the field, it is impossible to reach a robust conclusion about their conspecificity or otherwise.

Taxon *habenichti*.—Finsch (1912) described this form (from across northern New Guinea) as a full species, from a single specimen—hence it was much mistrusted by Rothschild & Hartert (1912)—with the simple diagnosis (our translation) 'general colouration like *P. macklotii* but at once distinguished by the brighter red nape' (score 1). Subsequent specimen material apparently vindicated Finsch, but the nape colour of BMNH 1939.12.9.3800 (from the range of *habenichti*) is barely distinguishable from that of BMNH 1934.10.21.98 (*macklotii*, from Batanta), and there seem to be no other plumage differences—the suggestion that the black breast-band is narrower than in *macklotii* (Irestedt *et al.* 2013) is not supported by material in AMNH—while mensurally *habenichti* is virtually identical to *macklotii*. Indeed, Pratt & Beehler (2015) recently remarked that *macklotii* and *habenichti* 'are not reliably identifiable by appearance or voice', so the validity of this taxon must lie in the balance.

Taxon *finschii*.—The description by Ramsay (1884) indicates that this form differs in only one respect from *macklotii* (including all its subspecies), namely in its blue *vs* green upperparts (score 3). Irestedt *et al.* (2013) suggested it is closest to *E. m. loriae* (with which it shares a dark brown hindcrown); measurements show it to be marginally larger, with a longer tail (effect size 2.0; score 2). A score of 5 indicates a relatively high degree of differentiation in this form.

Other taxa

Taxa long acknowledged as relatively weakly marked and treated by Irestedt *et al.* (2013) as either subspecies or synonyms were evaluated as follows.

Taxon *thompsoni*.—We did not see specimens of this form, from Culion and Calauit in the Philippines. It was accepted but considered 'probably not valid' by Mayr (1979) and, although also accepted by Dickinson & Christidis (2014), was determined to be a synonym of nominate *erythrogaster* by Irestedt *et al.* (2013), who described it as 'more or less intermediate between nominate *erythrogaster* and *propinqua*, blue on upperparts tending to be as extensive as in *propinqua* but less deep in colour, sometimes even paler than in nominate, which is also rather variable in this respect, but characters variable and taxon best included in *propinqua*'. We accept this synonymisation which, however, also involves the synonymisation of *propinqua*.

Taxon *propinqua*.—As an illustration of the dangers of small sample sizes, three out of the four characters used by Sharpe (1877) to distinguish this taxon were found by Everett (1895), on obtaining a larger series, to be invalid; the one character Everett considered dependable is its reduced amount of dorsal green. However, while this appears to be a trend, it is certainly not a constant (BMNH 89.1.20.19 from Taguso, Palawan, fully matches nominate *erythrogaster*), and we therefore could not comfortably assign it a score. Rothschild (1899) remarked that the distinctness of this form 'is very doubtful'; we agree, and prefer not to recognise it.

Taxon *obiensis*.—Hachisuka (1935) described this taxon as a subspecies of *E. rufiventris*, writing: 'Three males and one female collected by Doherty and Waterstradt, from Obi, are distinguished in having the breast a lighter blue, which is more extended over both sides of the breast'. However, White & Bruce (1986), Lambert (1996), Erritzoe (2003) and Irestedt *et al.* (2013) all synonymised

obiensis with *rufiventris*, finding it undiagnosable, but Mayr (1979) accepted it ('very near *rufiventris*') and Erritzoe & Erritzoe (1998) recognised it based on 'silvery wash on blue breast band and tail and legs larger than *rufiventris* and no blue collar (AMNH)'. The only specimen in Tring, BMNH 1903.6.2.44 (a female), shows a *fractionally* paler breast, but the Erritzoes' point about the blue collar is mistaken as *rufiventris* lacks this also; measurements of three male specimens put both tail and legs outside the range of 22 male specimens of *rufiventris*, but there is overlap in females. On balance the evidence base for this subspecies appears just too speculative for its recognition.

Taxon *inornata*.—The description of this taxon came just a year after (and doubtless in ignorance of) that of *rufiventris*; it is a synonym of the latter.

Taxon *cyanonota*.—This form differs from *rufiventris* by its blue *vs* green upperparts (echoing *finschi* from *macklotii*) (score 3). The claim that the crown is 'more pinkish-scarlet..., less saturated ferruginous' (Irestedt *et al.* 2013) is not supported by NHMUK material, but the crown shows some diffuse, semi-concealed blue feathering absent in *rufiventris* (score 1). Measurements are very close to *rufiventris*, but a larger sample is needed to determine if real differences exist.

Taxon *bernsteini*.—In describing this form (from Gebe), Junge (1958) clearly indicated its close morphological similarity to *cyanonota* (from Ternate), but 'seen in a series [six] the Gebe birds are slightly paler blue (more silvery blue) on the upperparts and breast [and] the throats are probably slightly paler...'; moreover, they are slightly longer-winged and -billed than *cyanonota* (Junge 1958). The scores here could not total more than 3, which exaggerates the differences between the two taxa as apparent in the RMNH material of each, and we recognise this form with mild reservations (although the notion that a population off the west coast of Halmahera would be taxonomically identical to one off the east coast, with *rufiventris* between them, is clearly debatable).

Taxon *kuehni*.—Rothschild (1899) established this form from the Kai Islands because 'the blue of the chest extends over the sides of the chest and breast (where there is a green patch in *P. macklotii*) and is continued in a narrow blue ring round the upper back', with apparently slightly longer feathers on the breast-sides and a greater frequency of blue in the crown. None of these characters is well supported in the NHMUK, RMNH or ZMB material, and the general tendency to synonymise the form is followed by Irestedt *et al.* (2013). Erritzoe & Erritzoe (1998) declared their agreement with this, but paradoxically provided (a) an entry for the form as if they judged it valid and (b) mensural data with good sample sizes which indicate it is shorter-winged and -tailed than *macklotii* (effect size for wing –1.88, score 1). However, we judge this character too weak to retrieve *kuehni* from synonymy.

Taxon *aruensis*.—Rothschild & Hartert (1901) separated this form from *macklotii* on account of its 'distinctly smaller' size, with wings of four adults 'averaging about 100' *vs* 106 in *macklotii* and no overlap; they cited Salvadori as supplying confirmatory evidence on another six Aru specimens. Moreover, Aru birds 'sometimes have a strong blue wash on the back'. Erritzoe & Erritzoe (1998), although failing to provide measurements for more than one bird of each sex, retained *aruensis*, but Irestedt *et al.* (2013) synonymised it with *macklotii*, the key to this being their Table S11 in which the mean wing length of *aruensis* proves to be only 2 mm shorter than that of birds from the Watubela and Kai Islands (although measurements are not discriminated by sex). Slightly hesitantly we side with the decision to synonymise.

Taxon *loriae*.—This form has a distinctly darker, less rufous-chestnut hindcrown and nape than nominate *macklotii* and all its subspecies except *finschii* (Rothschild & Hartert 1901, Erritzoe & Erritzoe 1998, Irestedt *et al.* 2013; score 2), with marginally larger dimensions in all but males' tails (no score); the hindcrown and nape are the same colour as in subspecies *finschii* (no score) but the back is green not blue (score 3).

Taxon *oblita*.—Rothschild & Hartert (1912) described this form from five specimens taken at 'Avera' on or near the Aroa River near Port Moresby in south-eastern New Guinea, distinguishing it from *macklotii* by its blue-tinted (or in one case all-blue) back, less bright and less red hindneck and slightly paler crown, and suggesting a resemblance to the smaller, brighter-naped form *kuehni* (Kai Islands), which is, however, now widely synonymised with *macklotii* (see above). Perhaps because of this Irestedt *et al.* (2013), without explanation, synonymised the form with *loriae*. However, Mayr & Rand (1937) pointed out that *oblita* 'appears quite different [from *macklotii*], with the back very bluish and the nape pale ochraceous brown', both of these characters setting it apart from *loriae*; the blue-tinted upperparts score 2, the paler nape at least 1, and we therefore retain it as a subspecies. (RMNH 121419 is labelled *oblita* and has the nape pale ochraceous-brown, but the upperparts are dull brownish-green, and the provenance, 'Boven Digoel', is in present-day southern West Papua, Indonesia, clearly outside the range of true *oblita*.)

Taxon *extima*.—This was described by Mayr (1955) as like *novaehibernicae* 'but larger', with 'the nape on... average paler, more rufous... the blue stripe on the crown less reduced and the back more bluish green'. Measurements suggest the size difference is minor (score 1), as is the slightly paler nape (1) and the more evident bluish coronal stripe (1), while difference in dorsal colour is not obvious; a score of 3 overstates the distinctiveness of this form.

Taxon *strenua*.—This was described by Elliot (1870) merely on the basis of its slightly larger bill; Mayr (1979) and Erritzoe & Erritzoe (1998) synonymised it with *macklotii*, while Irestedt *et al.* (2013) do not even mention it. The type in NHMUK reveals a bill that is barely any larger than the largest bill of *macklotii*, and the taxon is not valid.

Taxon *digglesi*.—The year after its tentative description this form was dismissed by Elliot (1870) as 'in no way different from *P. mackloti*', and it was widely treated as a synonym thereafter. However, Schodde & Mason (1999) considered this form 'evidently smaller and even lighter [= paler] and brighter than pallid *P. e. macklotii*...', suggesting that the small pale birds of the Trans-Fly region of New Guinea also belong in *digglesi*. Irestedt *et al.* (2013) therefore accepted the form and, owing to the sample sizes (62 birds from New Guinea, 25 from Australia) indicated as the basis of their judgement by Schodde & Mason (1999), we follow them; but four adult specimens from Queensland in NHMUK do not appear in the slightest different from a series from southern New Guinea, and in size *digglesi* is apparently very close to the synonymised *aruensis* (see above), so we recommend that further attention be given to the taxonomy of Australian birds. Indeed, although Schodde & Mason (1999) considered *digglesi* smaller than *macklotii*, the mensural data for it in Higgins *et al.* (2001) and for *macklotii* in Erritzoe & Erritzoe (1998) suggest a fractionally larger bird; even so, if *digglesi* is migratory, as the evidence generally suggests (Higgins *et al.* 2001), it is slightly puzzling that its wings are not notably longer than those of *macklotii*.

Taxon *yorki*.—This was described by Mathews (1912) as distinct from *macklotii* 'in having a smaller bill and smaller wing—100 mm'. Described from Cape York, it must be a synonym of *digglesi*.

DISCUSSION

The diagnoses of individual taxa by Irestedt *et al.* (2013) stopped short of itemising specific points of divergence from each of the other taxa under consideration. Here for the first time we provide such a review, inevitably at some length, since the full differentiation of 13 taxa from each other requires no fewer than 156 comparisons. In the

Plate 2. Two specimens of *E. caeruleitorques* (top in AMNH; bottom in RMNH) showing differences in crown colour and breast-band width in this taxon. [AMNH credit: NJC; Leiden credit: NJC/Naturalis Biodiversity Center]

course of this exercise the degree of morphological distinctiveness of the taxa that comprise the complex has become much clearer. Although no mechanism could be established under the Tobias criteria for providing a score for molecular evidence (since no threshold value for degree of genetic differentiation can be set), it is notable that morphological distinctiveness matched perceptions based primarily on DNA analysis in 13 (75%) out of 17 cases. Of the four taxa proposed for species status by Irestedt *et al.* (2013) but not supported by the Tobias criteria, the form *finschii* (which to Irestedt *et al.* 'represents a borderline case') showed the greatest distinctiveness, while *habenichti* proved rather weak, *piroensis* too uncertain on current evidence and *yairocho* undiagnosable. Over subspecies and synonyms we coincide with Irestedt *et al.* (2013) except to synonymise *propinqua* and to recognise, at least for now, the subspecies *oblita*, so that our suggested arrangement is as follows.

Philippine Pitta *Erythropitta erythrogaster* (includes *thompsoni*, *propinqua* and *yairocho*) – Philippine Is
Talaud Pitta *Erythropitta inspeculata* – Talaud Is
Sangihe Pitta *Erythropitta caeruleitorques* – Sangihe I
Siao Pitta *Erythropitta palliceps* – Siao I and Tahulandang I
Sulawesi Pitta *Erythropitta celebensis* – Sulawesi, Manterawu and Togian Is
Sula Pitta *Erythropitta dohertyi* – Banggai Archipelago and Sula Is
North Moluccas Pitta *Erythropitta rufiventris*
- *E. r. rufiventris* (includes *obiensis* and *inornata*) – North Moluccas
- *E. r. cyanonota* – Ternate
- *E. r. bernsteini* – Gebe I

South Moluccas Pitta *Erythropitta rubrinucha*
- *E. r. rubrinucha* – Buru
- *E. r. piroensis* – Seram

Papuan Pitta *Erythropitta macklotii*
- *E. m. macklotii* (includes *kuehni*, *aruensis* and *strenua*) – west & south New Guinea, including west Papuan Is
- *E. m. digglesi* (includes *yorki*) – Cape York Peninsula, Australia
- *E. m. habenichti* – north New Guinea (Weyland Mts east to Astrolabe Bay)
- *E. m. oblita* – south-east New Guinea west of Port Moresby
- *E. m. loriae* – extreme south-east New Guinea
- *E. m. finschii* – D'Entrecasteaux Archipelago

Louisiade Pitta *Erythropitta meeki* – Louisiade Archipelago
New Britain Pitta *Erythropitta gazellae* – South Bismarck Archipelago
Tabar Pitta *Erythropitta splendida* – Tabar I
New Ireland Pitta *Erythropitta novaehibernicae*
- *E. n. novaehibernicae* – New Ireland
- *E. n. extima* – New Hanover, Bismarck Archipelago

Plate 3. Three specimens of *E. erythrogaster 'yairocho'* (top and centre in RMNH, bottom the type in AMNH); note green breasts of RMNH specimens (one with white patch on throat), blue central breast and darker throat of the type. [Leiden credit: NJC/Naturalis Biodiversity Center; AMNH credit: M. Shanley/AMNH]

However, we do not pretend that this new arrangement of the Red-bellied Pitta complex is definitive. New insights from the field, particularly acoustic evidence, may provide the basis for further revisions of the taxonomy we propose here. Some of the taxa we accept as species are highly distinctive, but others only just meet the Tobias criteria. The differences between *E. caeruleitorques* and (a) *E. palliceps*, (b) *E. rufiventris* and (c) *E. meeki*, between *E. palliceps* and (a) *E. celebensis* and (b) *E. macklotii*, and between *E. macklotii* and *E. gazellae* are sufficient to establish the taxa as species, but further evidence may force new conclusions (we acknowledge that the deeper bill that clinches the split of *gazellae* from *macklotii*, scored as a medium character, is ostensibly improbable; but the sample sizes of males providing the evidence, 57 and 20 respectively, are compellingly large). In particular, diagnoses of taxa represented by very few specimens are inherently unstable, rendering decisions on taxonomic rank equally susceptible to alteration; for example, the crown colour and breast-band width of the only two specimens of *E. caeruleitorques* examined in this review were somewhat divergent (see Plate 2), while, as noted above, the characters defining '*yairocho*' proved elusive, some birds with all-green breasts (as in one or two *erythrogaster*), the type with a centrally blue breast (see Plate 3). In this last case, incidentally, Irestedt *et al.* (2013) also backed the split on the basis of the depth of the genetic differentiation and the fact that the form *inspeculata* appears to be more closely related to *erythrogaster* than is *yairocho*; however, not only is paraphyly

discounted by Tobias *et al.* (2010) as a final arbiter of taxonomic rank but also one Mindoro bird (i.e. *erythrogaster*) proved to be genetically close to *yairocho*, suggesting that a wider sampling effort is needed to determine the degree of phylogenetic structure in the Philippine archipelago.

Irestedt *et al.* (2013) invoked vocal differences to their cause by providing miniature sonagrams of songs of many taxa adjacent to other information in their Figures 5 and S3, but they made no attempt at an analysis of this acoustic evidence. Despite the differences suggested by these sonagrams, the songs of taxa in the Red-bellied Pitta complex tend, as several correspondents warned us, to sound very similar (two long, low, flat, guttural whistles, the first rising at the end), and one would imagine that the playback of any taxon's song might produce strong reactions in a living singer of another taxon in the complex; this consideration was presumably in Rheindt's (2010) mind when he expressed scepticism over the separation of the morphologically distinctive *E. dohertyi*. However, there is no reason why conservative song structure should overrule decisions based on other phenotypic evidence. Even so, a study of the variation in songs between taxa, taking full account of possible variation *within* taxa, would be a valuable exercise.

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